CHAPTER EIGHT

Nesting Success and Resource Selection of Greater Sage-Grouse

Nicholas W. Kaczor, Kent C. Jensen, Robert W. Klaver, Mark A. Rumble, Katie M. Herman-Brunson, and Christopher C. Swanson

Abstract. Declines of Greater Sage-Grouse (*Centrocercus urophasianus*) in South Dakota are a concern because further population declines may lead to isolation from populations in Wyoming and Montana. Furthermore, little information exists about reproductive ecology and resource selection of sage grouse on the eastern edge of their distribution. We investigated Greater Sage-Grouse nesting success and resource selection in South Dakota during 2006–2007. Radio-marked females were tracked to estimate nesting rates, nest success, and habitat resources selected for nesting. Nest initiation was 98.0%, with a maximum likelihood estimate of nest success of 45.6 ± 5.3%. Females selected nest sites that had greater sagebrush canopy cover and visual obstruction of the nest bowl compared to random sites. Nest survival models indicated that taller grass surrounding nests increased nest survival. Tall grass may supplement the low sagebrush cover in this area in providing suitable nest sites for Greater Sage-Grouse. Land managers on the eastern edge of Greater Sage-Grouse range could focus on increasing sagebrush density while maintaining tall grass by developing range management practices that accomplish this goal. To achieve nest survival rates similar to other populations, predictions from our models suggest 26 cm grass height would result in approximately 50% nest survival. Optimal conditions could be accomplished by adjusting livestock grazing systems and stocking rates.

Key Words: Centrocercus urophasianus, Greater Sage-Grouse, nest initiation, nest success, renesting, resource selection, sagebrush, South Dakota.

Kaczor, N. W., K. C. Jensen, R. W. Klaver, M. A. Rumble, K. M. Herman-Brunson, and C. C. Swanson. 2011. Nesting success and resource selection of Greater Sage-Grouse. Pp. 107–118 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage grouse) are a sensitive species for state and federal resource management agencies due to declining populations and degradation and loss of nesting habitat (Aldridge and Brigham 2001, Connelly et al. 2004, Schroeder et al. 2004). Estimated trends of male sage grouse lek counts in South Dakota declined steadily from 1973 to 1997. From 1997 to 2004, sage grouse populations may have increased slightly (Connelly et al. 2004). Isolation from populations in neighboring states raises additional concerns for sage grouse persistence in South Dakota (Aldridge et al. 2008).

Declines in sage grouse populations have resulted in several petitions to list sage grouse under the Endangered Species Act (ESA) of 1973 (Connelly et al. 2004). Currently, federal land management agencies are responsible for approximately 66% of the sagebrush landscape in the United States. Federal agencies such as the U.S. Bureau of Land Management (BLM) and U.S. Forest Service (USFS) are directed by administrative policy to manage public lands for sustained multiple use under the Federal Land Policy and Management Act (1976) and the Public Rangelands Improvement Act (1978). Currently, sage grouse are managed as a sensitive species by BLM and USFS, and their management should not result in further population declines of sage grouse, which could lead to listing under ESA. The South Dakota Department of Game, Fish, and Parks has identified sage grouse as a species of special concern (South Dakota Department of Game, Fish, and Parks 2006). Listing of sage grouse under the ESA could have major ramifications on the use and management of public lands in the western United States (Knick et al. 2003).

Nest success is one factor that can determine whether sage grouse populations increase or decrease (Braun 1998, Schroeder et al. 1999, Dinsmore and Johnson 2005). Yet information is lacking on the ecological requirements of nesting sage grouse in western South Dakota. The objectives of this study were to develop an understanding on the nesting ecology, success, and resource selection of sage grouse at the eastern edge of their range.

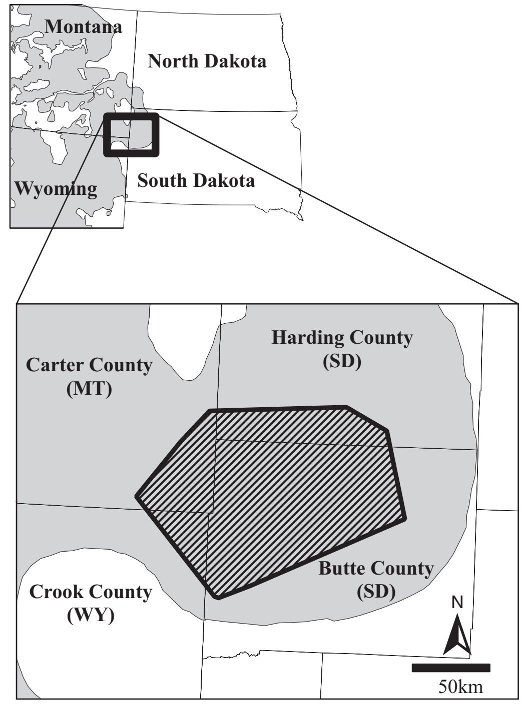

Figure 8.1. Location of study area for Greater Sage-Grouse in Butte, Carter, Crook, and Harding counties, 2006–2007. The hatched area encompasses all locations; the gray area is the current range of Greater Sage-Grouse (Schroeder et al. 2004).

STUDY AREA

The study was conducted within a 3,500 km^2 area in Butte and Harding counties, South Dakota; Crook County, Wyoming; and Carter County, Montana (44°44′ N to 45°20′ N, 103°15′ W to 104°21′ W; Fig. 8.1). Approximately 75% of the area was privately owned. The remaining 25% of the study area was managed by the BLM and State of South Dakota School and Public Lands Division. The area was predominately used for grazing, although small grain production also occurred. Open-pit mining for bentonite occurred at the south end of the study site on Pierre soils (C. Berdan, pers. comm.).

Vegetation consisted of short shrubs, mostly Wyoming big sagebrush (*Artemisia tridentata* spp.) and plains silver sagebrush (*A. cana* spp.). Other shrubs included broom snakeweed (*Gutierrezia sarothrae*), greasewood (*Sarcobatus vermiculatus*), and saltbushes (*Atriplex* spp.) (Johnson and Larson 1999). Common grasses included western wheatgrass (*Pascopyrum smithii*), Junegrass (*Koeleria macrantha*), bluegrass species (*Poa* spp.), green needle-grass (*Nassella viridula*), and Japanese brome (*Bromus japonicus*). Common forbs included western yarrow (*Achillea millefolium*), common dandelion (*Taraxacum officinale*), pepperweed (*Lepidium* *densiflorum*), and field pennycress (*Thlaspi arvense*) (Johnson and Larson 1999).

Temperatures in summer (May–August) averaged 20.1°C but can reach highs of 43.3°C (South Dakota State Climate Office 2007). During the months of March through June 2006 and 2007, the study area received approximately 14 cm and 22 cm of precipitation, 33% less and 5% more than the 58-year average of 21 cm (1956–2007; South Dakota State Climate Office 2007). Elevation ranges from 840 to 1,225 m above sea level with nearly level to moderately steep clayey soils over clay shale (Johnson 1976).

METHODS

Data Collection

We captured female sage grouse at or near six leks using large nets and spotlighting them from all-terrain vehicles each year between March and mid-April 2006 and 2007 (Giesen et al. 1982, Wakkinen et al. 1992). Females were weighed and equipped with a 22-g necklace-style transmitter; transmitters were approximately 1.4% of mean female sage grouse body mass and had a life expectancy of 434 days. Transmitters could be detected from a distance of approximately 2–5 km from the ground and were equipped with an 8-hour mortality switch. Females were classified as yearlings (<1 yr old) or adults (>1 yr old) based on primary wing feather characteristics (Eng 1955, Crunden 1963). The South Dakota State University Institutional Animal Care and Use Committee approved trapping and handling techniques, as well as study design (Protocol #07-A032).

We located radio-marked female sage grouse twice each week during the breeding, laying, and incubation periods. In the event we could not locate an individual from the ground, we searched the study area from a fixed-wing aircraft to obtain an approximate location. Once a female was believed to be incubating, we recorded four coordinates approximately 15 m away from the nest in the four cardinal directions with a Global Positioning System (GPS) receiver. We confirmed nest presence/absence during the subsequent visit. If a female was present on the second visit, we flushed her to determine clutch size. Our use of this method did not decrease nest survival for the immediate interval after the female was flushed from the nest. Nests were considered successful if ≥1 egg hatched. We calculated distances from nearest active display ground to nests, renests, and previous nests by the same bird using Hawth's Analysis Tool (Beyer 2004).

We characterized vegetation at nest sites after their fate was determined. Four 50-m transects were established radiating in the four cardinal directions from the nest bowl and four additional 5 m transects were established at the 45° intervals. A modified Robel pole was used to estimate visual obstruction (VOR) and maximum grass height at 1-m intervals from 0 m to 5 m ($n = 21$), and at 10-m intervals out to 50 m ($n = 20$) along each 50 m transect (Robel et al. 1970, Benkobi et al. 2000). We estimated sagebrush (*A. tridentata* spp. and *A. cana* spp.) density and height at 10-m intervals ($n = 80$) using the point-centered quarter method (Cottam and Curtis 1956). Vegetation canopy cover was estimated using a 0.10 m^2 quadrat at 1-m intervals to 5 m ($n = 44$) and at 2-m intervals along the long transects to 30 m ($n = 52$). We estimated percent canopy cover for total vegetation, grass, forb, shrub, litter, bare ground, and individual shrub and grass species (Daubenmire 1959). This method is amenable to collecting data on windy days and yields data that are similar (<3% difference for sagebrush) to the line-intercept method, but may provide more accurate estimates of cover (Floyd and Anderson 1987, Booth et al. 2006).

We measured an equal number of random sites within a 3-km buffer of capture leks to estimate resource selection. We navigated to the coordinates of random sites with a GPS and located the center of the transects over the nearest sagebrush because sage grouse usually nest beneath a shrub.

Data Analyses

Nesting Parameters

We used the multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test the null hypothesis that there were no differences between mass of female age-classes, clutch size of female age-classes, clutch size between first nests and renests, nest initiation date between years, distance among nests within a year, distance between nests between years (nest site fidelity), and distance to display grounds between years and age-classes of females. To avoid biasing estimates of nesting and renesting rates, we randomly selected one observation for females that nested both years. Chi-square goodness-of-fit tests were used to test for differences in nest initiation rates between years and between age-classes of females. Statistical significance was set at $\alpha \leq 0.05$. Egg hatchability was the proportion of eggs hatching from successful clutches.

Average grass height and VOR were calculated for each 1-m interval away from the nest to 5 m, at 10-m intervals from 10 to 50 m, and for the site at 0 to 50 m. We used a maximum likelihood estimator to estimate sagebrush density (Pollard 1971). We calculated average sagebrush height for each site from the sagebrush plants that were measured to estimate density. Canopy coverage values were recoded to midpoint values of categories, and these were summarized to an average for 0 to 5 m, 6 to 30 m, and for the site at 0 to 30 m (Daubenmire 1959). To reduce the number of variables in the vegetative dataset to a manageable level and identify biologically important variables to carry forward in the analyses, we used MRPP to identify variables that exhibited differences ($\alpha \leq 0.15$) between nest and random sites, and again between successful and failed nests (Boyce et al. 2002, Stephens et al. 2005). Two separate screen processes were conducted as some variables could be important for nest selection but may not have a measurable effect on nest success.

Resource Selection

We identified ten habitat variables from the nest site selection MRPP analyses (Table 8.1). We used these and a year effect to investigate sage grouse nesting resource selection. Variables included: percent total vegetation cover, grass cover, sagebrush cover, and litter; site averages for sagebrush height, grass height, and visual obstruction; grass height 0–5 m from the nest; visual obstruction at the nest; and visual obstruction 1 m from nest.

Year was included as a design variable in all resource selection candidate models. To reduce potential variable interaction in our models, variables that were correlated to one another ($r > 0.70$) were not included in the same model (e.g., total vegetation cover plus grass cover). We used an information theoretic approach with logistic regression to estimate the support for models evaluating resource selection at nest sites (Burnham and Anderson 2002, SAS Institute Inc. 2007). Due to a small sample size with respect to the number of parameters estimated ($n/K < 40$); we used the small-sample adjustment for Akaike's Information Criterion (AIC_c) to evaluate models (Burnham and Anderson 2002). We ranked our models based on differences between AIC_c for each model and the minimum AIC_c model (ΔAIC_c), and Akaike weights (w_i) to assess the weight of evidence in favor of each model and the sum AIC_c weight for each variable (Beck et al. 2006). In addition, we investigated the slope of the coefficient estimates (β) to determine variable effect. We evaluated the predictive strength of our models using a receiver operation characteristic curve (ROC); values between 0.7 and 0.8 were considered acceptable predictive discrimination and values higher than 0.8 were considered excellent predictive discrimination. Model goodness-of-fit was determined using a Hosmer–Lemeshow test (Hosmer and Lemeshow 2000).

Nest Success

We used the nest survival procedure in program MARK to evaluate environmental and biological factors that might influence nest survival (White and Burnham 1999, Dinsmore et al. 2002). We standardized nesting dates among years by using the earliest date we discovered a nest as the first day of the nesting season. We monitored nests over a 59-day period beginning 23 April and ending 20 June, which comprised 58 daily intervals of observations to be used in estimating daily survival rate (DSR) for the 27-day incubation period. We identified four variables from the MRPP analyses of nest success as having potential to impact nest success. These variables included: grass height at the site level, visual obstruction at the site level, litter cover at the site level, and forb cover at the nest bowl. The variables were then combined with daily precipitation, daily minimum temperature, bird age, stage of incubation, and year. We did not model nest survival associated with nesting attempt because of a small number of renests ($n = 10$), although they were included in the analysis to test for seasonal variation. Daily weather variables were obtained from the nearest daily weather station located at Nisland, South Dakota, ~50 km from the center of the study area (South Dakota State Climate Office 2007). To reduce the effect of variable interaction in our models, variables that were correlated ($r > 0.70$) were not included in the same model.

TABLE 8.1

Mean vegetation characteristics of nest sites and random sites between years for Greater Sage-Grouse in northwestern South Dakota, 2006–2007.

	Nest			Random			Pooled		
Variable	2006 (n = 34)	2007 (n = 39)	$P \leq$	2006 (n = 35)	2007 (n = 39)	$P \leq$	Nest (n = 73)	Random (n = 74)	$P \leq$
Total cover (%)[1]	61.1 (2.3)	75.1(2.0)	0.01	55.8 (2.4)	66.1 (2.4)	0.01	68.6 (1.7)	61.2 (1.8)	0.01
Litter (%)	7.6 (0.8)	7.1 (0.6)	0.79	6.5 (0.7)	6.1 (0.4)	0.88	7.4 (0.5)	6.3 (0.4)	0.01
Grass cover (%)[1]	24.2 (1.9)	31.4 (1.8)	0.01	21.1 (1.9)	25.8 (2.0)	0.21	28.1 (1.4)	23.6 (1.4)	0.01
Max grass hgt. (cm)[2]	23.4 (0.9)	29.5 (1.6)	0.01	20.4 (0.8)	25.0 (1.1)	0.01	26.7 (1.0)	22.8 (0.7)	0.01
Max grass hgt. 0–5 m (cm)[2]	25.7 (0.9)	30.9 (2.0)	0.02	20.3 (0.8)	24.3 (1.1)	0.01	28.5 (1.2)	22.4 (0.8)	0.01
Visual obstruction (cm)	5.5 (0.6)	11.1 (1.0)	0.01	3.7 (0.4)	5.1 (0.6)	0.14	8.5 (0.7)	4.4 (0.4)	0.01
Visual obstruction 0 m (cm)[3]	20.8 (1.7)	29.4 (1.8)	0.01	10.5 (1.1)	8.9 (1.0)	0.13	25.4 (1.3)	9.6 (0.7)	0.01
Visual obstruction 1 m (cm)[3]	7.3 (0.9)	13.7 (1.7)	0.01	3.7 (0.5)	4.1 (0.6)	0.45	10.7 (1.0)	3.9 (0.4)	0.01
Sagebrush cover (%)	10.3 (0.8)	10.1 (0.8)	0.75	6.3 (0.8)	6.3 (0.7)	0.98	10.2 (0.6)	6.2 (0.5)	0.01
Sagebrush hgt. (cm)	25.8 (1.2)	29.7 (1.6)	0.04	23.8 (1.0)	24.0 (1.0)	0.97	27.9 (1.7)	23.9 (1.3)	0.01

NOTE: All values are reported as $\bar{x} \pm$ (SE). Variables with the same superscript number were correlated ($r > 0.70$) and not modeled together.

We used an information theoretic approach to evaluate support for models that influenced DSR (Burnham and Anderson 2002). We began by developing base models that included female age-classes, year, and constant survival. From these base models, we further explored the degree to which habitat and weather variables improved model fit. We used back-transformed estimates of DSR to estimate effects of variables on nest survival for the best supported models (Dinsmore et al. 2002). We then plotted DSR versus simulated values of variables to determine the effect of variables independently from one another. Estimated standard error for nest survival over the 27-day nesting cycle was calculated using the delta method (Seber 1982).

RESULTS

Nesting Parameters

We captured and attached transmitters to 53 female sage grouse (28 yearlings and 25 adults); 29 individuals were included both years for the resource selection analyses. Adults weighed (1,664 ± 14 g, $\bar{x}$ ± SE; n = 43) more than yearlings (1,524 ± 16, n = 24; $P < 0.01$). There were no differences in female mass between years (P = 0.20; n = 67). Nest initiation rate for all females was 98.0% and did not differ significantly between years (P = 0.96; n = 67) or with female age-class (P = 0.92; n = 67). Renest initiation rate was 25.8% (8/31) and did not differ significantly between years (P = 0.19; n = 31) or female age-class (P = 0.62; n = 31). Females were more likely to renest if their first nest was lost early in the incubation period (P = 0.02; n = 31). The number of nest observation days for first nests was 7.9 ± 1.3 SE days (n = 8) for females that renested and 14.6 ± 1.8 SE (n = 23) days for females that did not renest.

Average date of nest initiation for successful first nests was 24 April ± 1.6 SE (n = 30) days, with adults initiating egg laying approximately 6.7 days earlier than yearlings (P = 0.02; n = 30). Average hatch date for first nests was 31 May ± 1.5 SE (n = 30) days. Average date of renest initiation was approximately 15 days later (9 May ± 2.6 SE days; n = 8) than first nests, with hatch date occurring 14 June ± 2.0 SE days. Clutch size differed between nesting attempts (first nests: 8.3 ± 0.2 SE eggs; renests: 6.4 ± 0.6 SE; $P < 0.01$; n = 64), but not by nest fate (P = 0.83), female age-class (P = 0.98), or year (P = 0.10).

One adult female in 2007 nested approximately 30.3 km from lek of capture but most females nested close to leks. In 2006, successful nests were significantly closer to an active lek (P = 0.04; n = 40) than failed nests (1.5 ± 0.3 km vs. 2.9 ± 0.5 km, $\bar{x}$ ± SE); however, there was no difference in 2007 (2.5 ± 0.5 km vs. 3.2 ± 0.7 km, P = 0.70; n = 39), or when both years were combined (2.1 ± 0.3 km vs. 3.0 ± 0.4 km, P = 0.13; n = 79). The distance that adults and yearlings nested from the nearest active lek did not differ significantly (2.2 ± 0.3 km vs. 3.3 ± 0.5 km, P = 0.08; n = 79). Sixty-eight percent of nests were within 3 km of a documented active lek, and 97% of nests were within 7 km.

Average distance between an individual's nest in 2006 to its nest in 2007 was 1.08 ± 0.40 SE km (n = 21). There was no difference in nest site fidelity between adults and yearlings (P = 0.65; n = 21) or between nests that either failed or were successful the first year (P = 0.47; n = 21). Mean distance between failed first nests and subsequent renests was 1.85 ± 0.55 SE km (n = 8). Successful renests (0.95 ± 0.36 SE km) were not significantly closer to first nests than failed renests (2.03 ± 0.91 SE km, P = 0.17; n = 8).

Resource Selection

Distribution of total cover, grass cover, grass height, visual obstruction, and sagebrush height differed between nest sites in 2006 and 2007 ($P < 0.05$; Table 8.1). In addition, all screened vegetative characteristics differed between nests and random sites (Table 8.1). The minimum AIC_c model (AIC_c weight = 0.39; Table 8.2) of nest site selection included sagebrush canopy coverage at the site level (β = 0.20, SE = 0.06) and visual obstruction at the nest (β = 0.22, SE = 0.04; Table 8.2). Increasing sagebrush cover by 5% increased the odds of use approximately 6.1 times. Increasing visual obstruction at the nest by 2.54 cm increased the odds of use 3.2 times. Predictive ability of the top model (ROC values) was excellent at 0.93 and the Hosmer–Lemeshow goodness-of-fit test was nonsignificant (P = 0.14), indicating acceptable model fit.

A second model including sagebrush canopy coverage, visual obstruction at the nest, and average

TABLE 8.2

Selected models from logistic regression analysis (n = 39 models) predicting Greater Sage-Grouse nest sites (n = 73) versus random sites (n = 74) in northwestern South Dakota, 2006–2007.

Model[a]	Log(L)	K[b]	Δ AICc[c]	w_i[d]
Sagebrush cover + visual obstruction 0 m	−50.80	5	0.00	0.52
Sagebrush cover + visual obstruction 0 m + max grass hgt. 0–5 m	−49.82	6	0.22	0.47
Visual obstruction 0 m	−57.50	4	11.26	0.00
Sagebrush cover	−89.14	4	74.54	0.00
Intercept only	−101.89	2	95.85	0.00
Year	−101.89	3	97.92	0.00

[a] For ease of interpretation, year variable was excluded from model column. See Kaczor (2008) for full model set.
[b] Number of habitat parameters plus intercept, SE, and year.
[c] Change in AIC_c value.
[d] Model weight.

TABLE 8.3

Selected models for daily nest survival of Greater Sage-Grouse in northwestern South Dakota, 2006–2007.

Model[a]	K[b]	AIC_c	Δ AIC_c[c]	w_i[d]
Max grass hgt. + litter	3	225.79	0.00	0.23
Max grass hgt. + litter + daily precip. + precip. lag	5	226.75	0.96	0.15
Max grass hgt. + litter + daily precip.	4	227.37	1.60	0.11
Max grass hgt. + litter + bird age	4	227.77	1.98	0.09
Constant	1	252.71	26.92	0.00

[a] See Kaczor (2008) for full model set.
[b] Number of variables plus intercept.
[c] Change in AIC_c value.
[d] Model weight.

grass height within 5 m also had strong support (AIC_c weight = 0.35). Sagebrush canopy coverage and visual obstruction at the nest obtained the highest summed AIC_c weights of 0.99. The combined model of sagebrush canopy cover and visual obstruction at the nest had the greatest support, but there was less support for a single-factor model, although beta estimates for the two variables were similar ($\Delta\beta = 0.03$).

Nest Success

Most nests were located under Wyoming big sagebrush (90%) or silver sagebrush (7%; $n = 79$). One nest was against a large boulder, and another was in a dense stand of prairie cordgrass (*Spartina pectinata*). Egg hatchability averaged 78.3 ± 2.1 SE % ($n = 513$). Constant nest survival rates with no covariates were 45.6 ± 5.3 SE %, but that was a poor model of DSR. The best model for DSR (AIC_c weight = 0.23) included grass height and litter cover (Table 8.3). Three other models were $\Delta AIC_c \leq 2$ units of the top model. Grass height had a positive association with DSR ($\beta = 0.15$, SE = 0.03; Fig. 8.2), whereas percent litter cover had a negative association on DSR ($\beta = -0.08$, SE = 0.03); both factors were present in all of models with $\Delta AIC_c < 2.0$.

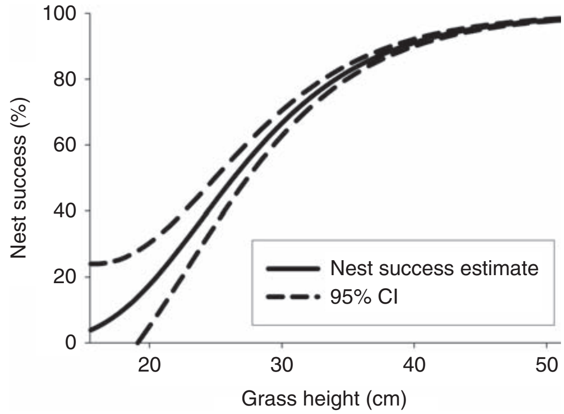

Figure 8.2. Effect of grass height on nest success of Greater Sage-Grouse in northwestern South Dakota, 2006–2007. Nest success estimates were derived from back-transformed beta estimates included in top model. Confidence intervals estimated from the delta method (Seber 1982).

The second-ranked model (AIC_c weight = 0.15) included grass height, litter, daily precipitation, and a 1-day lag of precipitation. Daily precipitation had a positive association with DSR (β = 29.5, SE = 40.4) and the 1-day lag of precipitation was negatively associated with DSR (β = –1.89, SE = 0.77). These variables were only included in supported models when combined with grass height and litter. The third- and fourth-ranked models both included grass height and litter along with the variables daily precipitation and bird age, respectively. Nest success differed between years from 37.7 ± 7.3 SE % in 2006 to 52.5 ± 7.2 SE % in 2007. However, adding a year effect to the top model did not improve model fit.

DISCUSSION

Our study of Greater Sage-Grouse on the easternmost portion of their range in South Dakota identified interesting aspects of sage grouse ecology that have not previously been documented. Female body condition was above average and nesting initiation rates were also high. Similar to other studies, sagebrush cover was an important variable in nest site selection, but at a much lower density than expected. Grass structure, which far exceeded range-wide estimates, played an important role in providing increased cover for successful nests (Connelly et al. 2004). Overall, nest success was within range-wide estimates, suggesting certain features of the habitat condition in South Dakota are productive for sage grouse.

Nesting Parameters

Nest initiation rates for sage grouse are generally low compared to other prairie grouse (Bergerud 1988). However, estimates of nesting initiation based on telemetry are probably underestimated in the literature, as follicular development indicated that at least 98.2% of females laid eggs the previous spring in Idaho (Dalke et al. 1963, Schroeder et al. 1999). Nonetheless, nest initiation rates were high in this study relative to range-wide estimates (Connelly et al. 2004). Females in our study were approximately 63 g (~4%) heavier than the average for 673 individuals in eight other studies (Schroeder et al. 1999). Heavier body mass in female Wild Turkeys (*Meleagris gallopavo*) increased the likelihood of breeding (Porter et al. 1983, Hoffman et al. 1996). Sage grouse exhibit considerable temporal variation in nest initiation rates between years, which may be related to nutrition before and during the breeding season (Hungerford 1964, Barnett and Crawford 1994, Moynahan et al. 2007). High rates of initiation suggest that habitat conditions in our study site were above average.

Renesting rates in sage grouse are highly variable (0–87%), and are linked to environmental effects and habitat quality (Schroeder 1997, Moynahan et al. 2007). Low renesting rates may be related to low primary productivity in the arid and semiarid environments occupied by sage grouse (Schroeder and Robb 2003). For example, Moynahan et al. (2007) found no renesting by sage grouse in dry years with little vegetative growth. In North Dakota, Herman-Brunson et al. (2009) reported 9.5% renesting in sage grouse. The relatively high proportion of renesting females in our study and greater female mass suggest that nesting habitat in South Dakota is of higher quality than elsewhere in sage grouse range. The inverse relationship between length of incubation and renesting propensity suggests that the condition of the female may decline as incubation progresses. An inverse relationship between the duration of incubation and renesting has also been shown elsewhere (Aldridge and Brigham 2001, Herman-Brunson 2009, Martin et al., this volume, chapter 17).

Nest Success

Sage grouse in South Dakota selected nest sites with higher sagebrush cover and placed their nests beneath sagebrush plants with greater horizontal cover (VOR) than random sites. Shrub density (correlated with sagebrush cover) and nest-bowl VOR were important predictors of sage grouse nest sites in North Dakota (Herman-Brunson et al. 2009). Connelly et al. (2000) recommended 15–25% sagebrush canopy coverage for nesting sage grouse, and this recommendation has been confirmed with a range-wide meta-analysis (Hagen et al. 2007). In South Dakota, nesting sage grouse selected for sagebrush with the highest densities and protective cover, but that was less than recommended values. In contrast to sagebrush, grass structure in South Dakota exceeds both management recommendations and range-wide averages (Connelly et al. 2000, Hagen et al. 2007). Western South Dakota forms a transition zone between the northern wheatgrass–needlegrass prairie that dominates most of the Dakotas and the big sagebrush plains of Wyoming (Johnson and Larson 1999). Thus, while South Dakota had less than expected sagebrush cover for sage grouse, the grass structure likely compensated for the low sagebrush densities in providing cover for nests. Grass structure is highly correlated with annual precipitation; therefore, periodic drought may reduce nest cover for sage grouse. Poor grazing management in areas with low sagebrush cover could reduce grass structure, which may have detrimental effects on sage grouse nesting.

Sage grouse nest success varies widely across the range, from 14.5% (Gregg 1991) to 70.6% (Chi 2004), and is generally believed to be related to habitat conditions (Connelly et al. 1991, Aldridge and Brigham 2002, Hagen et al. 2007). Our estimate of nest success was similar to that of other sage grouse studies (48%; Connelly et al. 2004), despite the fact that available sagebrush canopy coverage was less than other areas. Successful nests in our study had taller grass structures than failed nests. Thus, tall grass differentiated not only suitable nest sites, but also nesting success. Nesting cover also increased nest success in Alberta, and was suggested to provide ample nest concealment in both sagebrush and non-sagebrush overstories in Washington (Sveum et al. 1998, Aldridge and Brigham 2002). Although litter cover entered our models as being an important predictive variable for nest success, the impact litter actually has on nest success is unknown. Litter may be greater after productive growing seasons, or be lower after intensive grazing pressure (Hart et al. 1988, Naeth et al. 1991).

Our results suggest that some aspects of sage grouse habitat in our study area were conducive to maintaining sage grouse populations despite being outside of current management recommendations (Connelly et al. 2000). Although management recommendations were based on existing knowledge, our habitat also provided the necessary requirements for the nesting period, which may be an important consideration for land managers elsewhere in sage grouse ranges.

Management Implications

If sage grouse populations continue to decrease or remain listed as a sensitive species, sagebrush conservation and enhancement could be a top priority for land management agencies to enable sage grouse persistence in western South Dakota. Management for greater grass and sagebrush cover and height, and reduced conversion to tillage agriculture, could be encouraged to protect remaining habitats. Grazing by domestic sheep (*Ovis aries*) can reduce sagebrush cover (Baker et al. 1976), thereby reducing habitat quality for sage grouse. Domestic sheep grazing is not widespread in South Dakota, but was common on both private and public lands in our study area.

Range management practices that could increase sagebrush and grass cover and height include: rest-rotation grazing, where the rested pasture is not grazed until early July to allow for undisturbed nesting, or reduced grazing intensities or seasons of use to reduce impacts on sagebrush and grass growth (Adams et al. 2004). Land managers could develop grazing plans that leave or maintain grass heights ≥26 cm to try to maintain 50% nest success. In addition, we suggest annual grazing utilization not exceed 35% in order to improve rangeland conditions, particularly sagebrush cover (Holechek et al. 1999).

Wyoming big sagebrush typically recovers from a fire in 50–120 years (Baker 2006), and because of the restricted distribution and limited cover of sagebrush in South Dakota, we suggest limited use of prescribed fire or herbicides in areas with sagebrush.

ACKNOWLEDGMENTS

Funding for this study was provided by the Bureau of Land Management (ESA000013), U.S. Forest Service Rocky Mountain Research Station (05-JV-11221609-127), U.S. Forest Service Dakota Prairie National Grasslands (05-CS-11011800-022), and support from South Dakota State University. Field assistance was provided by C. Berdan, T. Berdan, B. Eastman, B. Hauser, T. Juntti, J. Nathan, S. Harrelson, and T. Zachmeier. A number of volunteers assisted during capture and radio-collaring of females and chicks. A. Apa assisted with training on trapping techniques. We also acknowledge and appreciate those land owners who granted us permission to conduct this study on their private lands. We thank D. Turner, J. Sedinger, and an anonymous reviewer for their comments on prior versions of this manuscript. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

Adams, B. W., J. Carlson, D. Milner, T. Hood, B. Cairns, and P. Herzog. 2004. Beneficial grazing management practices for sage-grouse (*Centrocercus urophasianus*) and ecology of silver sagebrush (*Artemisia cana*) in southeastern Alberta. Technical Report, Public Lands and Forests Division, Alberta Sustainable Resource Development. Pub. No. T/049.

Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537–543.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood-rearing habitat use in southern Canada. Journal of Wildlife Management 66: 433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of Greater Sage-Grouse persistence. Diversity and Distributions 14:983–994.

Baker, M. F., R. L. Eng, J. S. Gashwiler, M. H. Schroeder, and C. E. Braun. 1976. Conservation committee report on the effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–170.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114–118.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile Greater Sage-Grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070–1078.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.

Bergerud, A. T. 1988. Population ecology of North American grouse. Pp. 578–685 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. Wildlife Management Institute, Minneapolis, MN.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools> (10 January 2006).

Booth, D. T., S. E. Cox, T. W. Meikle, and C. Fitzgerald. 2006. The accuracy of ground-cover measurements. Rangeland Ecology and Management 59:179–188.

Boyce, M. S., P. R. Vernier, S. E. Nielson, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of Fish and Wildlife Agencies 78:139–156.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Chi, R. Y. 2004. Greater Sage-Grouse on Parker Mountain, Utah. M.S. thesis, Utah State University, Logan, UT.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage-grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521–524.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846–849.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811–841.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–64.

Dinsmore, S. J., and D. H. Johnson. 2005. Population analysis in wildlife biology. Pp. 154–184 *in* C. E. Braun (editor), Techniques for wildlife investigations and management. 6th ed. The Wildlife Society, Bethesda, MD.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Floyd, D. A., and Anderson, J. E. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221–228.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage-grouse in Oregon. M.S. thesis, Oregon State University, Corvallis, OR.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of Greater Sage-Grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(Supplement): 42–50.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282–286.

Herman-Brunson, K. H., K. C. Jensen, N. W. Kaczor, C. C. Swanson, M. A. Rumble, and R. W. Klaver. 2009. Nesting ecology of Greater Sage-Grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. Wildlife Biology 15:237–246.

Hoffman, R. W., M. P. Luttrell, and W. R. Davidson. 1996. Reproductive performance of Merriam's Wild Turkeys with suspected *Mycoplasma* infection. Proceedings of National Wild Turkey Symposium 7:145–151.

Holechek, J. L., H. Gomez, F. Molinar, and D. Galt. 1999. Grazing studies: what we've learned. Rangelands 21:12–16.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. John Wiley and Sons Inc., New York, NY.

Hungerford, C. R. 1964. Vitamin A and productivity in Gambel's Quail. Journal of Wildlife Management 28:141–147.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota and the northern Great Plains. South Dakota State University. Brookings, SD.

Johnson, P. R. 1976. Soil survey of Butte County, South Dakota. U.S. Department of Agriculture, South Dakota Agricultural Experiment Station, Brookings, SD.

Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection Greater Sage-Grouse in northwestern South Dakota. M.S. thesis, South Dakota State University, Brookings, SD.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late: conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Mielke, P. W., and K. J. Berry. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York, NY.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of Greater Sage-Grouse in northcentral Montana. Journal of Wildlife Management 71:1773–1783.

Naeth, M. A., A. W. Bailey, D. J. Pluth, D. S. Chanasyk, and R. T. Hardon. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems in Alberta. Journal of Range Management 44:7–12.

Pollard, J. H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27:991–1002.

Porter, W. F., G. C. Nelson, and K. Mattson. 1983. Effects of winter conditions on reproduction in a northern Wild Turkey population. Journal of Wildlife Management 47:281–290.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–298.

SAS Institute Inc. 2007. JMP version 7. Cary, NC.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933–941.

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). A. Poole and F. Gill, (editors), The Birds of North America No. 425. The Birds of North America, Inc., Philadelphia, PA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin and Company Ltd., London.

South Dakota Department of Game, Fish, and Parks. 2006. South Dakota comprehensive wildlife conservation plan. South Dakota Department of Game, Fish, and Parks, Wildlife Division Report 2006-08, Pierre, SD.

South Dakota State Climate Office. 2007. Office of the State Climatologist. <http://climate.sdstate.edu> (15 December 2007).

Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. M. Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4–12.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265–269.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.